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Contrasting effects of reduced incubation cost on clutch attendance by male and female European starlings

Michael J.L. Magrath[1,2,3)], **Thijs van Overveld**[2)] **& Jan Komdeur**[2)]

([1] Department of Zoology, University of Melbourne, Parkville VIC 3010, Australia;
[2] Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 14, 9750 AA Haren, Netherlands)

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Summary

In biparental birds, the relative contribution of the sexes to parental care can be viewed as a co-operative equilibrium that reflects the relative costs and benefits to each parent. If there are asymmetries in these costs or benefits, then any changes to the cost of care could result in a corresponding adjustment to their relative contribution. Incubation is a parental activity, shared in many species, which is costly both in terms of energy expenditure and time. In this study we manipulated the cost of incubation for pairs of European starlings (*Sturnus vulgaris*) by experimentally warming selected clutches to examine how this affected attendance by each parent. We found that total nest attendance did not differ between heated and control nests, although there was some evidence among heated nests that attendance declined with increasing effectiveness of the heater. Furthermore, relative male contribution was greater at heated than control nests resulting from the net effect of females tending to reduce, and males increase, attendance. We suggest that this shift in relative attendance may have been observed because females have a more developed brood patch and are more sensitive and responsive to clutch temperature than males. Consequently, females tended to reduce attendance at heated nests while males, with less reliable information on the clutch's thermal status, increased attendance to compensate for the reduction by the female. We also found that females at heated nests were lighter than at control nests, possibly because they were able to shed the additional fat reserves, a characteristic of incubating birds, earlier than females at control nests. We suggest that adjustment of clutch temperature in biparental species provides a valuable approach to investigating factors, including functional differences, asymmetries in brood value, and parental negotiation rules, that shape the roles of the sexes in incubation.

[3)] E-mail address: magrath@unimelb.edu.au

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Keywords: incubation, parental care, nest attentiveness, cost of incubation, compensation, biparental care, brood patch, European starling.

Introduction

In most socially monogamous birds, both male and female contribute substantially to one or more parental activities such as incubation, nestling feeding or offspring defence (Clutton-Brock, 1991). However, the relative contribution by the sexes to these activities varies dramatically both across and even within species (Skutch, 1957; Silver et al., 1985; Clutton Brock, 1991), and these differences remain poorly understood (Ketterson & Nolan, 1994; Møller, 2000).

Interspecific differences in the roles of parents can arise through specialisation of the sexes in particular activities (Breitwisch, 1989; Clutton Brock, 1991). For example, females typically play a greater role in incubation, while males often adopt the primary role in territorial defence, or may provision the incubating female with food (Clutton-Brock, 1991). Additionally, variation in parental effort, at both the population and individual level, may reflect differences in the value of the offspring to the parent (Trivers, 1972; Maynard Smith, 1977; Montgomerie & Weatherhead, 1988; Møller & Cuervo, 2000). Such asymmetries may arise if one sex, usually the female, has a lower probability of nesting again either in the current or future breeding seasons (Sargent & Gross, 1985). Furthermore, the relative value of the brood to males may vary with confidence of genetic parentage (Trivers, 1972; Westneat & Sherman, 1993; Whittingham & Dunn, 2001), or opportunity to gain addition social mates or extra-pair copulations (Westneat et al., 1990; Ketterson & Nolan, 1994; Magrath & Komdeur, 2003).

The optimal contribution by one parent should also depend on the level of investment by their partner, with a reduction in effort by one parent usually predicted to result in partial compensation by the other (Chase, 1980; Houston & Davies, 1985; Winkler, 1987; Wright & Cuthill, 1989; McNamara et al., 1999). Consequently, the relative contribution by the sexes to shared parental activities can be viewed as a co-operative equilibrium that reflects the relative costs and benefits to each individual (Trivers, 1972; Houston & Davies, 1985; Winkler, 1987). Any changes to the costs or benefits of these activities, therefore, may translate to a shift in their relative contribution (Trivers, 1972; Magrath & Komdeur, 2003).

In most cases, successful incubation requires the clutch to be maintained at temperatures of between about 34-38°C for the majority of the incubation period. Temperatures below this range will generally retard development, and if these sub-optimal conditions persist for prolonged periods, the embryo will eventually die (Webb, 1987). Consequently, incubating birds are not only constrained in the time available for alternative activities such as foraging (Bryan & Bryant, 1999; Creswell et al., 2004) or, in the case of males, gaining additional matings (Westneat et al., 1990; Magrath & Komdeur, 2003), but also incur the energetic cost of maintaining adequate egg temperatures (Drent et al., 1985; Williams, 1996; Tinbergen & Williams 2002). Furthermore, it has been shown that these costs associated with incubation can have subsequent effects on survival (Visser & Lessells, 2001) and reproduction (Reid et al., 2000).

A number of studies have attempted to investigate the cost of incubation by experimentally elevating nest and clutch temperature (see Reid et al., 1999). This manipulation should reduce both the energetic cost required to maintain adequate incubation temperature and also the rate at which eggs cool in the absence of a parent (Haftorn, 1988; Williams 1996). These studies reveal not only the expected reduction in energy expenditure of the incubator (Williams, 1996; Tinbergen & Williams 2002) but also changes to patterns of clutch attendance. In populations of great tit *Parus major* (Bryan & Bryant, 1999), pectoral sandpipers *Calidris melanotos* (Cresswell et al., 2004) and European starlings *Sturnus vulgaris* (Reid et al., 2000) in which only females incubated, clutch attendance increased at heated nests. This was attributed to the reduced foraging needs of the female because of her lower energy requirements. However, in the uniparental Belding's savanah sparrow, *Passerculus sandwichensis* (Davis et al., 1984), and pied flycatcher, *Ficedual hypoleuca* (Haftorn & Reinertsen, 1990), attendance by the female decreased in response to nest heating, although in these cases the clutch temperature was elevated beyond the physiological zero temperature of about 26°C, above which embryonic development can occur in the absence of an incubating bird (Webb, 1987).

In species with biparental incubation, the situation is further complicated by the potential for differences in the response of each parent to changes in incubation cost (Smith & Montgomerie, 1992). In general, decreased parental demand, such as smaller brood sizes and greater food availability, are predicted to result in greater declines in parental effort for males than

female because of the asymmetries in brood value and/or role specialisation (Trivers, 1972; Drent et al., 1985; Wright & Cuthill, 1989; Dunn & Robertson, 1992; Magrath & Komdeur, 2003). However, very few studies have examined the influence of nest heating, or even ambient temperature, on the relative contribution of the sexes to incubation in biparental species (Smith & Montgomerie, 1992; Reid et al., 1999; Conway & Martin, 2000).

In this study, we explored the effect of reduced incubation cost on clutch attendance by male and female European starlings. Starlings are facultatively polygynous, but males contribute substantially to both incubation and nestling feeding when breeding in pairs (Wright & Cuthill, 1989; Pinxten et al., 1993; Smith et al., 1995; Komdeur et al., 2002). Previous work shows that starling pairs typically attended the clutch for over 80% of daylight hours (Drent et al., 1985; Pinxten et al., 1993; Smith et al., 1995; Reid et al., 2002). Nest heating of starling pairs has been conducted previously by Drent et al. (1985) who found a decline in total clutch attentiveness, although the effect on the relative share of incubation was not reported. As clutch warming should reduce the energetic cost of incubation, we predict that the relative contribution of females will increase at heated nests because male attendance will become less important (see above).

We also assessed the effect of nest heating during incubation on female mass at the start of the nestling period. Female passerines are typically heavier when incubating than at other times in the reproductive cycle, apparently to minimise the risk of energy shortage during periods of adverse environmental conditions and help buffer against fluctuations in egg temperatures (Moreno, 1989). These additional energy reserves, however, appear to compromise flight ability and efficiency and are typically shed early in the nestling period (Slagsvold & Johansen, 1998; Kullberg et al., 2002). We predict that extra body reserves may be less important at heated nests because of the reduced energy expenditure and consequently, by the start of the nestling period, females from heated nests will be lighter than those at control nests.

Materials and methods

Study site and population

The study was conducted during April and May of 2000 on a nest-box breeding population of European starlings at Vosbergen, near Groningen, in the

northern Netherlands. Vosbergen is a country estate comprising 106 ha of mixed deciduous forest with surrounding pastures used for grazing. Nest-boxes were located within three distinct areas of the forest that were separated by over 500 m. These areas contained 52, 39 and 21 nest-boxes respectively. The average distance between nest-boxes was about 10 metres. In the year of the study, starlings occupied a total of 39 nest-boxes. Some birds were already colour marked from previous years, allowing easy identification and discrimination between the male and female of pairs. For those pairs where both individuals were unmarked during the incubation period ($N = 15$ of 25), the sexes were distinguished by distinctive bill colouration and plumage characteristics of breast and abdomen (Feare, 1984). Most females were trapped in the first two days of the nestling period for collection of morphometric data, including tarsus length and mass. All nest-boxes were monitored daily to establish those that were active and determine the presence of eggs and the start of incubation (determined by sensing egg temperature).

Nest heating

The interior temperature of nest-boxes was elevated using a custom designed electronic heating device. This device consisted of an aluminium plate (120× 120 mm square and 1.0 mm thick) onto which was bolted a heat emitting MOSFET transistor and a thermistor. The bottom surface of the heating plate was covered with a square of foam rubber 8 mm thick to minimise heat loss from the bottom surface of the plate. The 'heating plate' was connected by a 5 m cable to a thermostatic control circuit that allowed the plate to be maintained at a relatively constant pre-determined temperature. The control circuit was mounted in a water-proof housing and placed beneath leaf litter at the base of the focal nest-box tree, together with a 12 VDC, 55 Ah, deep-cycle battery that served to power the device.

The heating plate was adjusted to remain at about 38°C and placed beneath the nesting material inside the nest-boxes. Calibration trials conducted prior to the experiment using fresh quail eggs revealed that the effect of the heater on egg temperature inside the nest-box varied with ambient temperature and depth of nest lining material between plate and egg (Figure 1). During the periods of observation in the field, ambient temperature varied between 8-25°C, so we estimated that clutch temperatures would typically have been elevated by between 5-10°C above ambient in the absence of an incubating bird, though we did not record egg temperature during incubation.

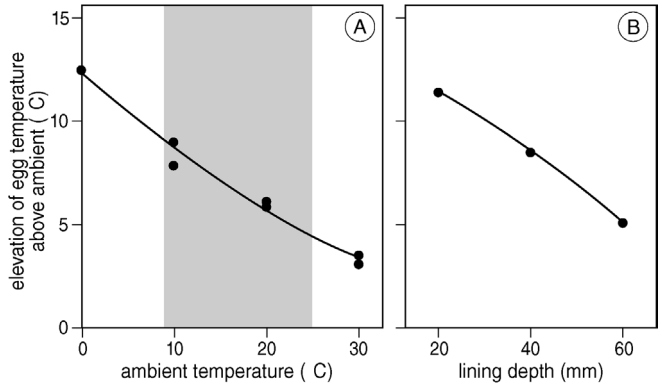

Figure 1. Calibration trials conducted in an incubator showing the effect of the nest heater on egg temperature elevation in relation to (A) ambient temperature and (B) depth of nest lining material. The grey area in (A) indicates the range of ambient temperatures encountered during field observation sessions.

Experimental design and observations

Heating plates were placed beneath the nesting material of 10 'heated' and 15 control nest boxes within several days of clutch completion. Heated nests were warmed for a period of at least one day prior to observation, and for at least four consecutive days during the course of the incubation period. Observations were conducted in sessions of 90 min duration, starting five min after arrival at the observation location. Each heated and control nest was observed for at least one session (mean = 2.2; range 1-4) between 0700-1200 h to determine attendance of each parent when the clutch was between 7-11 days old. On most observation mornings, data were collected concurrently from at least one heated and one control nest to ensure the data in each group were derived from a similar period of the season. All nest observation sessions ($N = 55$) were conducted between April 26 and May 8 and most (85%) between April 28 to May 2.

Boxes were observed from a distance of about 50 m using telescopes to allow detection and identification of individuals as they arrived at and departed the nest-box. Ambient temperature was also recorded at the start of each observation to permit control for variation in attendance associated with ambient temperature. The depth of the nest lining, from the centre of the nest down to the heating plate, was measured using a ruler and recorded to the nearest half centimetre.

Data analyses

Attendance at the nest during each observation session was derived for each parent (individual attendance) and pair (total attendance) and expressed in minutes per hour. Unfortunately, the average period of nest attendance (bout) or absence (recess) for individual birds could not be reliably derived as estimates based only on complete bouts or recesses within the 90-minute observation session underestimated the mean duration of these events.

Nests owned by males that were identified as polygynous (one heated and two control nests) were excluded from analysis because these males were dividing their parental activities between two nests.

As we had multiple, but a variable number of observation sessions for most nests, attendance patterns were analysed using the multilevel mixed-modelling procedure in MLwiN 1.10 (Rasbash et al., 2000) to account for the hierarchical and unbalanced structure of our data. For these analyses, nest identity was specified as a random term at level two with each observation for that nest at level one. Normal response models were constructed, as attendance data were distributed normally. Each model was derived using backward elimination of possible explanatory variables and their interaction terms. The significance of explanatory variables was determined by calculating the change in model deviance (which approximates the χ^2 distribution) as each term was eliminated from the final model. Final models included a constant together with any statistically significant ($p < 0.05$) explanatory variables. Non-significant interaction terms were not included in the model summary tables unless they were of specific interest.

Results

Nest attendance

Nests of socially monogamous starling pairs were attended by either parent for an average period of 46.9 ± 9.0 (SD) min/h ($N = 22$ nests) during observation sessions. There was no difference in this total attendance period between heated and control nests (Table 1; Figure 2). However, among heated nests there was a positive correlation between total attendance and depth of nest lining material, a pattern that was absent among control nests (Table 1; Figure 3). There was no difference between heated and control nests in the

Table 1. Model summaries examining the effect of nest heating, along with clutch and environmental variables, on clutch attendance by (a) pairs and (b) male and female European starlings. Summaries were derived from the normal response mixed-modelling procedure in MLwiN with two levels: nest identity ($N = 22$ nests) and observation session ($N = 46$). The effect of nest lining depth was examined in the subset of nests ($N = 16$ nests, 38 observation sessions) for which these data were available. In model (b) males were assigned the value of one and females zero.

Dependent variable	Explanatory terms	Coeff	χ^2	df	p
(a) Attendance by pair (min/h)	Heating treatment	−0.37	0.01	1	0.92
	Ambient temperature	−0.16	0.11	1	0.74
	Clutch age	0.80	0.99	1	0.32
	Clutch size	3.22	1.88	1	0.17
	Lining depth	2.23	3.92	1	0.05
	Heating treatment * lining depth	4.48	3.97	1	0.05
(b) Attendance by individual (min/h)	Heating treatment	0.26	0.01	1	0.92
	Sex	−15.67	35.7	1	<0.001
	Heating treatment * Sex	12.76	6.82	1	0.009
	Ambient temperature	−0.21	0.56	1	0.45
	Clutch age	0.04	0.14	1	0.96
	Clutch size	0.99	0.47	1	0.49

likelihood of containing unhatched eggs ($\chi^2 = 0.61$, $p = 0.43$, $N = 22$ nests).

Females were more attentive than males at both the heated and control nests (Table 1; Figure 2). However, the relative contribution by males was greater at heated than control nests (Table 1; Figure 2).

Nest heating and female body mass

Females captured and weighed early in the nestling period at heated nests ($N = 7$) were significantly lighter than females at control nests ($N = 12$), both in absolute terms (74.7±1.1 (SE) vs 77.7±0.8 g; $F_{1,17} = 4.7$, $p = 0.04$) and relative to their body size (comparing residuals of mass over tarsus; $F_{1,17} = 6.32$, $p = 0.02$). This provides support for the idea that females at heated nests shed additional body reserves earlier than females at control nests because of the reduced energetic cost and time spent incubating.

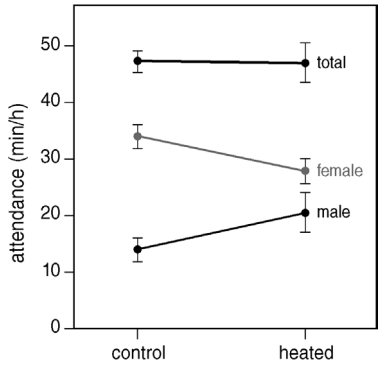

Figure 2. Incubation attendance by males and females in socially monogamous pairs of European starlings at heated ($N = 9$) and control ($N = 13$) nests. Estimates for mean attendance (± SE) were derived using a normal response mixed-modelling procedure.

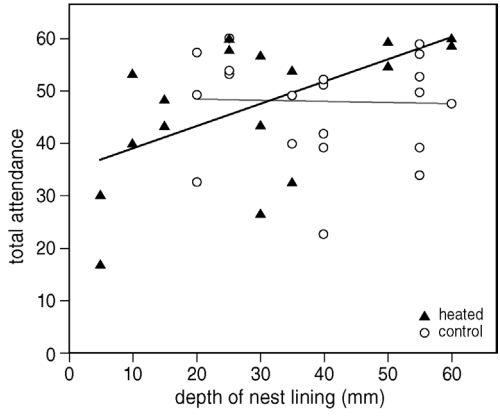

Figure 3. Incubation attendance by socially monogamous pairs of European starlings at heated ($N = 7$) and control ($N = 9$) nests in relation to depth of the nest lining material. Points show values for each observation session ($N = 16$ for heated nests and 21 for control nests) while lines represent the estimated slopes derived from a normal response mixed modelling procedure (black line = heated nests; grey line = control nests).

Discussion

Similar to the findings of previous studies on incubation attendance in social monogamous starlings (Drent et al., 1985; Pinxten et al., 1993; Komdeur et al., 2002; Reid et al., 2002), we found that females performed a greater share of incubation than males. However, we found that the relative contribution by males was greater at nests that were heated than at control nests. This result

is opposite to our original expectation that if the energetic cost of incubation was reduced (by warming nests), the relative contribution of males would decline.

This prediction was based on the argument that if the cost of care declines, male help should become less important to the success of the brood (see Introduction). This idea has previously received empirical support in a number of contexts where the cost of care was likely to have varied (e.g., Dunn & Robertson, 1992; Smith & Montgomerie, 1992; Komdeur et al., 2002). However, an assumption of this prediction is that relative male care should only decline if they have alternative avenues of reproductive success, unavailable to females, such as gaining additional partners or matings (Westneat et al., 1990; Møller, 2000; Magrath & Komdeur, 2003).

In the year of this study, the population of starlings breeding in the Vosbergen nested highly synchronously. Of the 29 females, 27 started laying within the five days from April 21-25. Consequently, the opportunity for males to gain extra-pair fertilisations once their incubation period commenced was likely to have been scarce. Moreover, no females confirmed as unpaired were observed in the colony during nest observation sessions, so the likelihood of attracting additional social mates also appeared to be minimal. Under these conditions, therefore, the lack of a reduction in the male's share of clutch attendance was perhaps not surprising. However, the observed *increase* in relative male care requires explanation.

We suggest that this increase in male care may stem from differences between the sexes in their sensitivity to the temperature of the clutch. In most species with biparental incubation, including the European starling (Cramp & Perrins, 1994; unpubl. data), females have a more developed brood patch than males (Skutch, 1957; White & Kinney, 1974; Deeming, 2002). Aside from the effective transfer of heat to eggs, the brood patch also appears to be important for assessing egg temperature using an array of thermo-receptors located on the bare skin (White & Kinney, 1974; Haftorn & Reinertsen, 1982, 1990; Zerba & Morton, 1983). Consequently, females are likely to have superior information about the thermal status and requirements of the clutch than males.

Most previous studies that have investigated patterns of incubation attentiveness have identified egg temperature as an important, though not the only, influence on the duration of incubation bouts in female birds (Reid et al., 1999; Conway & Martin, 2000; Deeming, 2002). Some studies show that

bout duration is negatively related to egg temperature at the start of the bout, while others indicate that the conclusion of an incubation bout is associated with the attainment of a particular threshold temperature (White & Kinney, 1974; Zerba & Morton, 1983; Davis et al., 1984; Drent et al., 1985; Haftorn & Reinertsen, 1990). This link between clutch temperature and attentiveness could, therefore, explain the reduction in attentiveness by females at heated nests, where egg temperatures would increase more rapidly when attended and cool more slowly when unattended. But how does this account for the apparent increase in male attentiveness at heated nests?

Notably, previous work relating egg temperature to clutch attentiveness has been conducted almost exclusively on female birds, usually of species in which only the female incubates. As the males starlings have only a rudimentary brood patch they may be far less responsive to the thermal status of the clutch. Consequently, clutch attentiveness among males may be dictated to a significant degree by the attendance behaviour of the female. Indeed, in the study on incubation patterns in the starling by Drent et al. (1985), females were found to be more effective at warming eggs, while males played a more ancillary role of maintaining egg temperatures in the females absence (but see Reid et al., 2002). Therefore, the increase in attentiveness by males may represent compensation for the reduced attentiveness by the female. At least partial compensation for shortfalls in the effort by one parent are predicted by theory (Chase, 1980; Winkler, 1987; McNamara et al., 1999) and have been reported in a range of studies in relation to brood feeding rate (e.g., Houston & Davies, 1985; Wright & Cuthill, 1989; Wright & Dingemanse, 1999; Sanz et al., 2000; but see Schwagmeyer et al., 2002). Compensation would also be anticipated during the incubation period, although we are unaware of any studies that have explicitly tested this idea during the incubation phase of the reproductive cycle.

The effect of temperature elevation on female attentiveness was also apparent in this study in relation to depth of the nest lining. We found that total attendance was lower in nests with shallower nest lining among the heated but not control nests. At heated nests, egg temperatures would have been greater at nests with less lining material, as shown in Figure 1, because of their closer proximity to the heating plate. Indeed, at nests with less than 20 mm of lining material, eggs were probably maintained above the physiological zero temperature (PZT; about 26°C) for most of the time even in the absence of an incubating bird. Although we did not document changes in

lining depth during the experiment, it appeared that nesting material was actively being removed from some of the heated nests. This may have been in response to the nest becoming too warm, as some species are known to adjust nesting material in relation to changing environmental conditions (Szentirmai & Szekely, 2002). Alternatively, the birds may have discovered that the removal of material resulted in an increase in clutch temperature. Clearly, concurrent information on actual egg temperatures during incubation would have been useful to examine in more detail how temperature related to attendance in both sexes.

Interestingly, Reid et al. (1999) studying the effect of nest warming in a population of female-only incubating starlings found that attentiveness increased at heated nests. In this case, however, the nest temperature was elevated by a smaller margin, as the aim was primarily to slow the rate of egg cooling. Consequently, given the cool prevailing ambient temperatures at that location (mean of about 10.5°C), clutches would soon have fallen below the PZT in the absence of the female, regardless of the nest warming procedure. In contrast, in our study, the absence of the female would rarely have resulted in the clutch declining below the PZT because nests were heated to a greater extent and both sexes contributed to incubation resulting in greater total attentiveness. The contrasting outcomes of these studies, however, do serve to highlight the fact that changes to attendance patterns in response to nest heating (and possibly ambient temperature — see Conway & Martin, 2000) may well depend on the number of birds incubating and the extent to which nest temperatures are elevated.

In conclusion, this study demonstrates how changes to the cost of providing parental care can influence the relative effort by the sexes. In this case, the shift in relative contribution to incubation may have resulted from differences in the sensitivity of male and female starlings to clutch temperatures, coupled with a compensatory response to reduced partner participation. If so, an experiment involving the cooling of nests may produce the opposite effect, with females increasing and males reducing attentiveness, again in contrast to our original expectation. It would seem, therefore, that experiments involving the manipulation of clutch temperature in biparental birds should provide a rewarding approach to examining the processes of parental co-operation and negotiation.

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